Advances in and Prospects for *Actinidia* Viruses

Guoding Zhang,^{1,2} Bixin Bai,^{1,2} Ming Xu,³ Yuling Liu,^{1,2} Yunfeng Wu,^{1,2,†} and Lei Zhao^{1,2,†}

¹ State Key Laboratory of Crop Stress Biology for Arid Areas, College of Plant Protection, Northwest A&F University, Yangling 712100, Shaanxi, China

² Key Laboratory of Plant Protection Resources and Pest Management, Ministry of Education, College of Plant Protection, Northwest A&F University, Yangling, 712100, Shaanxi, China

³ Shaanxi Rural Science and Technology Development Center, Xi'an 710054, Shaanxi, China

Abstract

Kiwifruit (*Actinidia* spp.) is an economically important fruit crop worldwide. Before 2010, kiwifruit viruses had not received much attention; since then, more than 20 viruses infecting kiwifruit have been discovered. Some of these viruses cause severe yellowing, mosaic, necrosis, ringspots, and other symptoms on leaves, seriously impacting yield and quality. Many of these viruses are widely distributed. This review summarizes recent research advances in the

identification, genomic variation, distribution, transmission, detection, incidence, prevention, and control of kiwifruit viruses and proposes directions for future research. Using virus-tested propagation material is the most economical and effective method for controlling kiwifruit viruses.

Keywords: *Actinidia* virus, kiwifruit virus, virus elimination

Kiwifruit cultivation and production are distributed across 23 countries and regions on 5 continents worldwide. Among these countries, China, Italy, New Zealand, Chile, and Greece have the largest cultivation areas (Ferguson 2015; Huang 2009; Huang and Ferguson 2001). In the past 10 years, the global kiwifruit cultivation area and yield have grown rapidly, and kiwifruit has become one of the world's most consumed fruit. China is the largest kiwifruit-producing country in terms of both yield and acreage (Ferguson 2015). In 2019, China's kiwifruit cultivation area was 290,000 ha, with a total output of 3 million tons. Kiwifruit is cultivated in 21 provinces, autonomous regions, and municipalities in China, with Shaanxi, Sichuan, Guizhou, Hunan, and Jiangxi Provinces producing the most fruit (Fig. 1). Among these provinces, Shaanxi ranks first, with approximately 40% of the total kiwifruit industry in China. The northern foot of the Qinling Mountains in Shaanxi Province is the world's largest contiguous kiwifruit-growing area (Figs. 2, 3, and 4).

Rapid expansion of the cultivation area of kiwifruit and a large amount of uncontrolled grafting and cutting propagation have led to frequent outbreaks of kiwifruit disease (Figs. 5 and 6) (Sawada and

Fujikawa 2019). In recent years, numerous studies have reported kiwifruit virus diseases worldwide (Blouin et al. 2013; Chavan et al. 2013; Zhao et al. 2019, 2020, 2021; Zheng et al. 2017). Many known viruses have recently been detected in kiwifruit, and multiple novel viruses have also been found (Blouin et al. 2013; Zhao et al. 2021). This review summarizes recent research advances in kiwifruit viruses and proposes research directions for the future.

Viral Species and Symptoms of Viral Infection in Kiwifruit

Apple stem grooving virus (ASGV) was first detected in kiwifruit in 2003 when woody kiwifruit cuttings were exported to New Zealand from Shaanxi, China (Clover et al. 2003). This was the first virus confirmed in kiwifruit. Since 2011, scientists in New Zealand, Italy, and China have discovered 22 viruses in kiwifruit, 11 of which are new viruses; for the other 11 viruses, kiwifruit is a new host (Blouin et al. 2012, 2013; Chavan et al. 2013; Pearson et al. 2011; Veerakone et al. 2018; Zhao et al. 2019, 2020, 2021; Zheng et al. 2017). In total, 23 viruses belong to 8 families and 15 genera, while 2 viruses have not been assigned to a specific genus (Table 1).

These 23 viruses are divided into four categories based on their symptoms. The first group includes viruses that cause chlorosis, mosaic, ring-spot, and mottling symptoms on leaves of both *Actinidia deliciosa* and *A. chinensis*. Viruses in this group include ASGV, cucumber mosaic virus (CMV), potato virus X (PVX), *Actinidia emaravirus* 2 (AcEV-2), citrus leaf blotch virus (CLBV), *Actinidia chlorotic ringspot-associated virus* (AcCRAV), and *Actinidia seedborne latent virus* (ASbLV) (Fig. 7A and B) (Blouin et al. 2013; Veerakone et al. 2018; Zheng et al. 2017). Among these viruses, CLBV, AcCRAV, and ASbLV are unique in that they can cause vein clearing or vein yellowing in addition to mosaic patterns, ringspots, and chlorosis (Fig. 7C). The second group of viruses consists of *Actinidia* yellowing ringspot virus (AYRSbV). After infection, this virus causes obvious symptoms of yellowing and ringspots on the leaves of both *A. deliciosa* and *A. chinensis* (Fig. 7D) (Zhao et al. 2021). When the infection is severe, the whole tree can

[†]Corresponding authors: Y. Wu; wuyf@nwsuaf.edu.cn, and L. Zhao; zhaolei5105@126.com

G. Zhang and B. Bai contributed equally to the present study.

Funding: This study was supported by the Key Research and Development Program of Shaanxi Province (2021NY-040), the Postdoctoral Innovation Talents Support Program (BX20190289), the General Financial Grant from the China Postdoctoral Science Foundation (2019M663840), and the National College Students Innovation and Entrepreneurship Training Program (S202110712317X).

The author(s) declare no conflict of interest.

Accepted for publication 20 December 2021.

exhibit a yellow color, which is relatively easy to distinguish from other infection symptoms. Notably, the yellowing caused by infection with AYRSpV is uneven, which can be visually distinguished from the yellowing caused by a lack of nutrients. Changes in symptoms in successive months after AYRSpV infection were reported in detail in a previous article (Wu et al. 2022). The third group of viruses includes those that cause mild or no symptoms on the leaves of both *A. deliciosa* and *A. chinensis* after infection (Fig. 7E). These viruses include cucumber necrosis virus (CNV), ribgrass mosaic virus (RMV), turnip vein clearing virus (TVCV), Actinidia virus X (AVX), alfalfa mosaic virus

(AMV), Actinidia virus A (AcVA), Actinidia virus B (AcVB), and Actinidia virus C (AcVC) (Blouin et al. 2012, 2013; Zhao et al. 2020). The fourth group of viruses cause leaf necrosis and ringspots upon infection of *A. chinensis* (Fig. 7F). The viruses that cause these symptoms are Actinidia virus 1 (AcV-1), pelargonium zonate spot virus (PZSV), tomato necrotic spot associated virus (TNSaV), tomato necrotic spot tospovirus (TNSV), and cherry leaf roll virus (CLRV) (Blouin et al. 2013, 2018; Wang et al. 2016; Wang et al. 2017). The symptoms of Actinidia yellowing virus 1 (AcYV1) and Actinidia yellowing virus 2 (AcYV2) are not yet known (Zhao et al. 2021).

According to the symptoms caused by these viruses, AYRSpV, PZSV, and CLRV infection are highly pathogenic to kiwifruit (Blouin et al. 2013; Zhao et al. 2021). CMV, AcCrAV, TNSaV, TNSV and AcV-1, which cause mosaic, ringspots, and chlorosis, should also be considered for future research (Blouin et al. 2013, 2018; Wang et al. 2016; Wang et al. 2017; Zhao et al. 2021; Zheng et al. 2017). The remaining viruses have a relatively small effect on kiwifruit (Blouin et al. 2013).

Regardless of the kind of virus, different ecological environments affect symptoms differently. Most plant viruses show optimal growth at temperatures below 30°C; therefore, infected kiwifruit tend to show obvious symptoms between spring and summer. We found that AcVA, AcVB, and AcVC, which caused only mild symptoms in summer, often caused obvious leaf distortion symptoms on newly developed young leaves of kiwifruit when the temperature was suitable in spring, and CLB infection in spring also caused similar symptoms (Fig. 7G). When summer temperatures rise above 30°C for a period of time, the symptoms of the viral infection gradually abate. AYRSpV is no exception; after a period of high summer temperatures, most of the leaves of a yellowed plant will slowly return to

Fig. 1. Main distribution of kiwifruit cultivation in China. Red circles represent the main kiwifruit growing areas. The number of red circles represents the size of the kiwifruit growing area. This is a map of some parts of China, and it shows that kiwifruit are mainly distributed in the central and southern parts of China. Only provinces with cultivation areas greater than 5,000 ha are indicated.

Fig. 2. Kiwifruit orchard at the northern foot of the Qinling Mountains in Shaanxi Province.

Fig. 3. Bagged kiwifruit in a kiwifruit orchard before ripening.

Fig. 4. A and B, Unbagged kiwifruit before ripening.

normal, leaving only a few areas of some leaves with white spots (Wu et al. 2022). Notably, most kiwifruit plants in the field are infected by two or more viruses, and the resulting symptoms are often mixed and more severe (Fig. 7H). In addition, nutrient deficiencies can sometimes cause symptoms similar to those of a viral infection. In summary, the symptoms of suspected viral infection in field-cultivated kiwifruit are complex and variable.

Fig. 5. A and B, Kiwifruit pruning. The pruning process may cause the spread of the virus.

Genomic and Molecular Variation of Kiwifruit Viruses

The genomes, virus particle shapes, and sizes of 23 kiwifruit viruses are shown in Table 1. Most viral genomes are composed of a single RNA molecule. In contrast, the AMV, CMV, PZSV, and AYRSpV genomes are each composed of three RNA molecules; the AcCRaV genome is composed of five RNA molecules; and the AcEV-2 genome is composed of six RNA molecules. The particles of these viruses range from spherical to bacilliform and flexuous to rigid.

We previously studied the molecular variation in AcVA, AcVB, AcVC, AcCRaV, ASGV, CMV, PVX, and CLBv (Liu et al. 2019a; Zhao et al. 2019, 2020, 2021). A phylogenetic tree of complete coat protein (CP) gene sequences revealed some genetic variability in the AcVA, AcVB, AcVC, CLBv, and AcCRaV isolates of kiwifruit in Shaanxi Province. However, there was no obvious molecular variation within the CP genes of ASGV, CMV, and PVX isolates from Shaanxi kiwifruit (Zhao et al. 2019). Y. X. Wang et al. (2018) also studied the molecular variation of ASGV isolates and found that they had little variation in kiwifruit.

We also sequenced the genomes of two AcV-1 isolates and one ASbLV isolate. The genomes of the two Chinese isolates of AcV-1 had 68.3 and 68.4% genomic identity with Italian AcV-1 isolates (Zhao et al. 2021), and the genome of the ASbLV isolate from China had 76.2% genomic identity with isolates from New Zealand. In addition, Wang et al. (2020) sequenced the genomes of three Chinese isolates of AcV-1, and these genomes shared 60 to 87% genomic identity with the AcV-1 isolate reported here. Wen et al. (2020) sequenced the genomes of four Chinese isolates of AcV-1, and these genomes shared 63.6 to 79.3% genomic identity with the AcV-1 K75 isolate. These results suggest that both the AcV-1 and ASbLV genomes are highly variable.

Distribution and Transmission of Kiwifruit Viruses

Kiwifruit viruses have been reported in only four countries: China, New Zealand, Italy, and South Korea (Table 2). It is possible that many more viruses have been detected in other countries but have not yet been reported. In recent years, many new kiwifruit viruses have been found and may exist in many countries. In addition, viruses such as ASGV, RMV, AMV, CLRV, CMV, CLBv, PVX, and TVCV are widely distributed around the world, and it is possible that some of these viruses may infect kiwifruit in additional countries (Blouin et al. 2013; Hadidi and Barba 2011).

The transmission vectors of CLBv, AcVA, AcVB, AcVC, AcV-1, ASbLV, AcEV-2, AcCRaV, AYRSpV, AcYV1, AcYV2, ASGV, AVX, RMV, and TVCV have not been reported. Transmission vectors have been reported for the remaining viruses but the identification of vectors in kiwifruit is lacking (Blouin et al. 2013; Wang et al. 2017). We have investigated many possible insect vectors that may transmit kiwifruit viruses in kiwifruit orchards in Shaanxi, China; although there are many leafhoppers in these orchards, the number of other potential insect vectors is very small. We performed virus tests on the possible vectors but none has been confirmed to carry kiwifruit viruses. Therefore, we suspect that the kiwifruit

Fig. 6. A and B, Kiwifruit grafting and C, cutting propagation. Kiwifruit grafting and cutting propagation are two important ways of virus transmission. Grafting (B) caused the spread of virus and the grafted plants showed symptoms of leaf yellowing.

Table 1. Species, hosts, and geographical distributions of kiwifruit viruses

Virus species ^a	Acronym	Classification	Genome (nucleotides)	Particle size (nm)	Symptoms in kiwifruit	Host range	Geographical distribution	References
Known								
<i>Potato virus X</i>	PVX	<i>Alphaflexiviridae</i> , <i>Potexvirus</i>	6,435	Flexuous, 12–13 × 470–580	Mosaicism	Solanaceae and kiwifruit	Worldwide	Martelli et al. 2007; Zhao et al. 2019
<i>Apple stem grooving virus</i>	ASGV	<i>Betaflexiviridae</i> , <i>Capillovirus</i>	6,465	Flexuous, 12 × 620–700	Interveinal mottling, chlorotic mosaics and ringspots	Apple, pear, cherry, citrus, kiwifruit and some other host	Worldwide	Clover et al. 2003; Y. X. Wang et al. 2018; Zhao et al. 2012
<i>Citrus leaf blotch virus</i>	CLBV	<i>Betaflexiviridae</i> , <i>Citrivirus</i>	8,747	Flexuous, 12–15 × 960	Associated with vein clearing and mild mottling on leaves and interveinal chlorosis	Citrus and kiwifruit	Worldwide	Vives et al. 2001; Pearson et al. 2011; Chavan et al. 2013; Zhu et al. 2016
<i>Alfalfa mosaic virus</i>	AMV	<i>Bromoviridae</i> , <i>Alfamovirus</i>	RNA1: 3,644; RNA2: 2,593; RNA3: 2,037	Bacilliform, 18 × 30–57	Mild symptoms on <i>A. chinensis</i>	Wide host range	Worldwide	Pearson et al. 2011; Loesch-Fries 2021
<i>Cucumber mosaic virus</i>	CMV	<i>Bromoviridae</i> , <i>Cucumovirus</i>	RNA1: 3,357; RNA2: 3,050; RNA3: 2,016	Spherical, 29	Chlorosis on <i>A. chinensis</i>	Wide host range	Worldwide	Pearson et al. 2011; D. Wang et al. 2018; Hirsch and Moury 2021
<i>Pelargonium zonate spot virus</i>	PZSV	<i>Bromoviridae</i> , <i>Anulavirus</i>	RNA1: 3,383; RNA2: 2,435; RNA3: 2,659	Spherical, 25–35	Concentric chlorotic/necrotic rings and line patterns	Pelargonium, tomato, pepper, artichoke, and kiwifruit	Italy	Biccheri et al. 2012; Bujarski et al. 2012; Blouin et al. 2013
<i>Tomato necrotic spot tospovirus</i>	TNSV	<i>Bunyaviridae</i> , <i>Tospovirus</i>	Unknown	Unknown	Brown ringspots and necrotic spots	Tomato and kiwifruit	China	Wang et al. 2017
<i>Tomato necrotic spot associated virus</i>	TNSaV	<i>Bunyaviridae</i> , <i>Tospovirus</i>	Unknown	Unknown	Brown ringspots and necrotic spots	Tomato and kiwifruit	China	Blouin et al. 2013; Wang et al. 2016
<i>Cherry leaf roll virus</i>	CLRV	<i>Secoviridae</i> , <i>Nepovirus</i>	7,918, 6,360	Spherical, 28	Necrotic spots on leaves, bark cracking and cane wilting in severe infections	Wide host range	Worldwide	Woo et al. 2012; Blouin et al. 2013; Thompson et al. 2017
<i>Cucumber necrosis virus</i>	CNV	<i>Tombusviridae</i> , <i>Tombusvirus</i>	4,701	Spherical, 16–18, 23–28, 32–35	Symptomless	Cucumber, lettuce, tomato and kiwifruit	Italy, New Zealand, Canada	Pearson et al. 2011; Alam et al. 2017
<i>Ribgrass mosaic virus</i>	RMV	<i>Virgaviridae</i> , <i>Tobamovirus</i>	6,311	Rigid rod, 18 × 300	Symptomless	Wide host range	Worldwide	Pearson et al. 2011; Chavan et al. 2012; Blouin et al. 2013
<i>Turnip vein clearing virus</i>	TVCV	<i>Virgaviridae</i> , <i>Tobamovirus</i>	6,311	Rigid rod, 18 × 300	Symptomless	Wide host range	Worldwide	Blouin et al. 2013
New								
<i>Actinidia virus X</i>	AVX	<i>Alphaflexiviridae</i> , <i>Potexvirus</i>	6,851	12 × 485	Latent	Kiwifruit and blackcurrant	New Zealand	James and Phelan 2016
<i>Actinidia virus A</i>	AcVA	<i>Betaflexiviridae</i> , <i>Vitivirus</i>	7,670	Flexuous, 15 × 750	Associated with leaf clearing and ringspots but can be latent	Kiwifruit	China, Italy, New Zealand	Blouin et al. 2012; Zheng et al. 2014; Zou et al. 2020

(Continued on next page)

^a Known = known viruses for which kiwifruit was found to be a new host and New = new viruses found in kiwifruit.

Table 1. (Continued from previous page)

Virus species ^a	Acronym	Classification	Genome (nucleotides)	Particle size (nm)	Symptoms in kiwifruit	Host range	Geographical distribution	References
<i>Actinidia virus B</i>	AcVB	<i>Betaflexiviridae</i> , <i>Vitivirus</i>	7,488	Flexuous, 15 × 750	Associated with leaf clearing and ringspots but can be latent	Kiwifruit	China, Italy, New Zealand	Blouin et al. 2012; Zheng et al. 2014; Zou et al. 2020
<i>Actinidia virus C</i>	AcVC	<i>Betaflexiviridae</i> , <i>Vitivirus</i>	7,668	Flexuous, 15 × 750	Chlorotic spots and wrinkles	Kiwifruit	China	Zhao et al. 2020
<i>Actinidia seedborne latent virus</i>	ASbLV	<i>Betaflexiviridae</i> , <i>Prunivirus</i>	8,192	Flexuous, unknown	Vein chlorosis and mottling	Kiwifruit	China, New Zealand	Veerakone et al. 2018
<i>Actinidia emaravirus 2</i>	AcEV-2	<i>Bunyaviridae</i> , <i>Emaravirus</i>	RNA1: 7,079; RNA2: 2,252; RNA3: 1,387; RNA3: 1,514; RNA5: 1,744; RNA6: 1,233	Unknown	Leaf mottling	Kiwifruit	China	Wang et al. 2020
<i>Actinidia chlorotic ringspot-associated virus</i>	AcCRaV	<i>Bunyaviridae</i> , <i>Emaravirus</i>	RNA1: 7,061; RNA2: 2,267; RNA3: 1,678; RNA4: 1,644; RNA5: 1,476	Spherical, 100	Ringspots, vein yellowing and chlorotic spots	Kiwifruit	China	Zheng et al. 2017
<i>Actinidia yellowing ringspot virus</i>	AYRSpV	<i>Bromoviridae</i> , <i>Ilarivirus</i>	RNA1: 3,357; RNA2: 2,318; RNA3: 2,229	Spherical, 26–35	Yellow ringspots and chlorosis	Kiwifruit	China	Zhao et al. 2021
<i>Actinidia virus 1</i>	AcV-1	<i>Closteroviridae</i>	18,848	Flexuous, unknown	Chlorotic and necrotic rings	Kiwifruit	China, Italy	Blouin et al. 2018; Peng et al. 2019; Wen et al. 2019
<i>Actinidia yellowing virus 1</i>	AcYV1	<i>Secoviridae</i> , <i>Waikavirus</i>	12,149	Spherical, 25–30	Unknown	Kiwifruit	China	Zhao et al. 2021
<i>Actinidia yellowing virus 2</i>	AcYV2	<i>Tombusviridae</i>	3,936	Spherical, 32–35	Unknown	Kiwifruit	China	Zhao et al. 2021

viruses in China are transmitted mainly by grafting or by rubbing wounds caused by farming practices.

Detection and Incidence of Kiwifruit Viruses

The methods commonly used for virus detection include enzyme-linked immunosorbent assay (ELISA), reverse-transcription (RT)-PCR, loop-mediated isothermal amplification (LAMP), deep sequencing, and host identification (Blouin et al. 2013; Cao et al. 2019; Liu et al. 2019b; Yang et al. 2019). Among them, ELISA, RT-PCR, and LAMP are relatively simple and are the most reported methods for virus detection. RT-PCR is the main method used for kiwifruit virus detection (Blouin et al. 2013; Zhao et al. 2021). ELISA and LAMP are also used but antibodies are not available for many kiwifruit viruses, and the LAMP detection method is currently only reported for CLB (Blouin et al. 2013; Liu et al. 2019b). Blouin et al. (2013) reported RT-PCR detection primers for CLB, AcVA, AcVB, AMV, ASGV, AVX, CLRV, CMV, CNV, PZSV, RMV, and TVCV. Peng et al. (2020) reported a multiplex RT-PCR assay for the simultaneous detection of CLB, AcVA, AcV-1, and AcCRaV. This detection system amplified specific DNA bands at a 10⁻⁴ dilution of cDNA in multiplex RT-PCR. Zhao et al. (2021) also reported primer sequences for simplex RT-PCR detection of many kiwifruit viruses. Because the genomes of these viruses vary greatly, the reported primer sequences may not be the most suitable for kiwifruit virus detection in different countries or regions, thus resulting in the virus not being detected. In addition, these reported primers may not be suitable for viruses present in all kiwifruit varieties, and some primers will amplify nonspecifically, producing heterozygous bands during the RT-PCR detection of viruses present in some kiwifruit varieties. Therefore, the multiplex

RT-PCR method reported by Peng et al. (2020) could be used to detect CLB, AcVA, AcV-1, and AcCRaV, and the LAMP method reported by Liu et al. (2019b) could be used to detect CLB. The primer sequences reported by Blouin et al. (2013) and Zhao et al. (2021) can be used for the detection of other kiwifruit viruses.

Previously, we studied the incidence of AcVA, AcVB, AcVC, ASGV, CLB, AcCRaV, CMV, AcV-1, ASbLV, AcYV1, AcYV2, and AYRSpV infection in kiwifruit samples with virus-like symptoms from Shaanxi (Zhao et al. 2021). The incidence of viral infection varied depending on the type of virus and the *Actinidia* sp. Among the viruses that we detected, AcV-1, CLB, AcVA, AcVB, and AcCRaV were relatively common in different kiwifruit-growing regions and among different kiwifruit cultivars; incidence of viral infection ranged from 30.5 to 43.8%, and from 11.8 to 27.9% for the remaining seven viruses. Incidence of AcVB, AcCRaV, ASGV, CMV, CLB, AcYV1, AcYV2, and AcV-1 infection in *A. deliciosa* was higher than in *A. chinensis*, and incidence of AcVA, AcVC, AYRSpV, and ASbLV infection in *A. chinensis* was similar to *A. deliciosa*. In addition, most symptomatic leaves were found to be infected by at least two viruses. Incidence of viral infection of kiwifruit in the field in Shaanxi was especially high for AcV-1, CLB, AcVA, AcVB, and AcCRaV, which should be given particular attention by kiwifruit growers, kiwifruit virus researchers, and the government.

Effects of Viruses on the Yield and Quality of Kiwifruit

There are few reports about the effects of kiwifruit viruses on fruit yield and quality. In the field, most viruses have some impact on the growth of kiwifruit but no major growth impediment has been found (Blouin et al. 2013; Zhao et al. 2021). However,

infection with the newly identified virus AYRSpV causes yellowing of the whole kiwifruit plant, which seriously affects yield and quality (Wu et al. 2022). We found that AYRSpV infection reduced the chlorophyll content of 'Hayward' kiwifruit by 74.6 to 76.6%, fruit yield by 14.5 to 24.1%, sugar-to-acid ratio by 50.1 to 50.6%, and fruit dry matter content by 1.7 to 1.8% (Wu et al. 2022). The significant decrease in chlorophyll affects photosynthesis and carbohydrate synthesis, thus affecting the yield and dry matter content of the fruit. AYRSpV infection affected both the number of fruit produced and the average weight of a single fruit. The acid content significantly increased after AYRSpV infection, which seriously affected fruit quality. This yield reduction causes direct economic losses. The average output of each infected plant of Hayward was reduced by 3.6 kg. With approximately 1,200 trees planted per hectare and the price of marketable Hayward fruit at U.S.\$0.47/kg, the resulting direct economic losses are U.S.\$2.030/ha of land in total (Wu et al. 2022).

Prevention and Control of Kiwifruit Viruses

Kiwifruit viruses infect kiwifruit systemically. The prevention of kiwifruit viral infection is more effective than treating infected plants. Using certified virus-free propagation material is the most economical and effective method for controlling kiwifruit viruses. To date, although our group has conducted related research, there have been no reports of methods for eliminating kiwifruit virus from infected plants. We are currently working on the field use of virus-indexed kiwifruit propagation material.

Previous work suggests that grafting may be an important mode of viral infection in kiwifruit in the field (Blouin et al. 2013; Zhao et al. 2021). Therefore, detecting infected scions and rootstocks before kiwifruit grafting is important. Propagation with infected scions from infected stocks should be avoided. Growers should not use scions or rootstocks from plants with leaf symptoms such as yellowing, chlorosis, mosaicism, curling, or shrinkage for grafting even when there is no virus detection.

For field-grown kiwifruit infected with a virus, it is costly and labor intensive to replace plants with virus-tested plants. Management should be strengthened for these parts of orchards. Kiwifruit plants with symptoms of AYRSpV, PZSV, and CLRV infection should be removed and destroyed immediately to prevent viral spread (Blouin et al. 2013; Zhao et al. 2021). The disinfection of pruning tools should be performed when branch pruning occurs every year to prevent viral transmission through the branch pruning process. In addition, tomato, tobacco, and other crops susceptible to kiwifruit viruses should not be planted in the vicinity of kiwifruit orchards to prevent the spread of CMV, TNSaV, PVX, and TNSV through cross infection.

Conclusion and Prospects

Because knowledge of kiwifruit viruses is limited, viral infection of cultivated kiwifruit is often ignored by growers. Traditional kiwifruit cultivation modes easily spread the viruses, and orchard pruning or grafting propagation may cause viral spread. These methods result in high incidence of infection by many kiwifruit viruses in the field (Zhao et al. 2019, 2020, 2021), which seriously affects yield. Viral infection also accumulates, causing damage over many years; the longer the infection lasts, the more serious the damage may be. Therefore, for the kiwifruit industry, viral disease is a major threat. A previous study by our team found that AYRSpV infection could cause serious yellowing symptoms in kiwifruit, leading to decreases in yield and quality. Research on kiwifruit viruses started late, lagging behind virus research on apple, pear, grape, citrus, and other fruit tree viruses. Virus elimination technology for apple, grape, and citrus crops has matured, and the use of virus-tested propagation material when planting these crops is increasing. Virus-indexing of kiwifruit plants will be an important research direction in the future. For growers, the detection of kiwifruit viruses and the use of virus-tested propagation material should become an important, widely available tool in the future.

Fig. 7. Leaf symptoms of field-grown *Actinidia deliciosa* and *A. chinensis* kiwifruit plants infected with different Actinidia viruses. **A**, Leaf infected with apple stem grooving virus and cucumber mosaic virus (CMV) showing mosaic and chlorosis symptoms; **B**, leaf infected with CMV and citrus leaf blotch virus (CLBV) showing mosaic and chlorosis symptoms; **C**, leaf infected with CLBV and Actinidia seedborne latent virus (ASbLV) showing yellow vein and crinkle symptoms; **D**, leaf infected with Actinidia yellowing ringspot virus (AYRSpV) showing yellow ringspot symptoms; **E**, leaf infected with Actinidia virus A (AcVA) showing chlorosis symptoms; **F**, leaf infected with AcV-1 showing ringspot and chlorosis symptoms; **G**, leaf infected with AcVA, Actinidia virus B, and CLBV showing malformation and crinkle symptoms; and **H**, leaf infected with AYRSpV, Actinidia yellowing virus 1, AcV-1, and CLBV showing yellow and crinkle symptoms.

Table 2. Distribution of kiwifruit viruses in different countries

Country	Number of viruses	Virus	References
China	16	Actinidia virus A, Actinidia virus B, Actinidia virus C, Actinidia emaravirus 2, Actinidia chlorotic ringspot-associated virus, Actinidia yellowing ringspot virus, Actinidia yellowing virus 1, Actinidia yellowing virus 2, Actinidia virus 1, Actinidia seedborne latent virus, tomato necrotic spot associated virus, cucumber mosaic virus, citrus leaf blotch virus, potato virus X, tomato necrotic spot tospovirus, apple stem grooving virus	Peng et al. 2019; Wen et al. 2019; Wang et al. 2016; Wang et al. 2020; Zheng et al. 2014; Zheng et al. 2017; Zhao et al. 2019; Zhao et al. 2020; Zhao et al. 2021
New Zealand	12	Actinidia virus A, Actinidia virus B, apple stem grooving virus, cucumber necrosis virus, ribgrass mosaic virus, alfalfa mosaic virus, cherry leaf roll virus, cucumber mosaic virus, citrus leaf blotch virus, turnip vein clearing virus, Actinidia virus X, Actinidia seedborne latent virus	Pearson et al. 2011; Blouin et al. 2013; Alam et al. 2017; James and Phelan 2016; Veerakone et al. 2018
Italy	6	Actinidia virus A, Actinidia virus B, cucumber mosaic virus, cucumber necrosis virus, pelargonium zonate spot virus, Actinidia virus 1	Pearson et al. 2011; Alam et al. 2017; Blouin et al. 2013; Blouin et al. 2018
South Korea	2	Actinidia virus A, Actinidia virus B	Cho et al. 2017

Literature Cited

- Alam, S. B., Reade, R., Theilmann, J., and Rochon, D. 2017. Evidence for the role of basic amino acids in the coat protein arm region of Cucumber necrosis virus in particle assembly and selective encapsidation of viral RNA. *Virology* 512:83-94.
- Biccheri, R., Babini, A. R., Blouin, A. G., Lanzoni, C., Pisi, A., Poggi, P. C., Credi, R., Laghi, L., Rocculi, P., Rubies, A. C., Pearson, M. N., and Ratti, C. 2012. Pelargonium zonate spot virus infecting kiwifruit plants in Italy. In: *Proc. 22nd Int. Conf. Virus and Other Graft Transmissible Diseases of Fruit Crops*, Rome, Italy.
- Blouin, A. G., Biccheri, R., Khalifa, M. E., Pearson, M. N., Pollini, C. P., Hamiaux, C., Cohen, D., and Ratti, C. 2018. Characterization of *Actinidia virus 1*, a new member of the family *Closteroviridae* encoding a thaumatin-like protein. *Arch. Virol.* 163:229-234.
- Blouin, A. G., Chavan, R. R., Pearson, M. N., MacDiarmid, R. M., and Cohen, D. 2012. Detection and characterisation of two novel vitiviruses infecting *Actinidia*. *Arch. Virol.* 157:713-722.
- Blouin, A. G., Pearson, M. N., Chavan, R. R., Woo, E. N. Y., Lebas, B. S. M., Veerakone, S., Ratti, C., Biccheri, R., MacDiarmid, R. M., and Cohen, D. 2013. Viruses of kiwifruit (*Actinidia* species). *J. Plant Pathol.* 95:221-235.
- Bujarski, J., Figlerowicz, M., Gallitelli, D., Roossinck, M. J., and Scott, S. W. 2012. *Bromoviridae*. Pages 965-976 in: *Virus Taxonomy: Ninth Report of the International Committee on Taxonomy of Viruses*. A. M. Q. King, M. J. Adams, E. B. Carstens, and E. J. Lefkowitz, eds. Elsevier, San Diego, CA, U.S.A.
- Cao, M., Zhang, S., Li, M., Liu, Y., Dong, P., Li, S., Kuang, M., Li, R., and Zhou, Y. 2019. Discovery of four novel viruses associated with flower yellowing disease of green Sichuan pepper (*Zanthoxylum armatum*) by virome analysis. *Viruses* 11:696.
- Chavan, R. R., Blouin, A. G., Cohen, D., and Pearson, M. N. 2013. Characterization of the complete genome of a novel citrivirus infecting *Actinidia chinensis*. *Arch. Virol.* 158:1679-1686.
- Chavan, R. R., Cohen, D., Blouin, A. G., and Pearson, M. N. 2012. Characterization of the complete genome of ribgrass mosaic virus isolated from *Plantago major* L. from New Zealand and *Actinidia* spp. from China. *Arch. Virol.* 157:1253-1260.
- Cho, S. Y., Kim, H., and Yi, S. I. 2017. First report of *Actinidia virus A* and *B* infecting *Actinidia chinensis* in South Korea. *Plant Dis.* 101:1560.
- Clover, G. R. G., Pearson, M. N., Elliott, D. R., Tang, Z., Smales, T. E., and Alexander, B. J. R. 2003. Characterization of a strain of *Apple stem grooving virus* in *Actinidia chinensis* from China. *Plant Pathol.* 52:371-378.
- Ferguson, A. R. 2015. Kiwifruit in the world-2014. *Acta Hort.* 1096:33-46.
- Hadidi, A., and Barba, M. 2011. Economic impact of pome and stone fruit viruses and viroids. Pages 1-7 in: *Virus and Virus-Like Diseases of Pome and Stone Fruits*. A. Hadidi, M. Barba, T. Candresse, and W. Jelkmann, eds. American Phytopathological Society, St. Paul, MN, U.S.A.
- Hirsch, J., and Moury, B. 2021. Cucumber mosaic virus (*Bromoviridae*). Pages 371-382 in: *Encyclopedia of Virology* (Fourth Edition), Vol. 3. D. Bamford and M. Zuckerman, eds. Academic Press, San Diego, CA, U.S.A.
- Huang, H., and Ferguson, A. R. 2001. Review: Kiwifruit in China. *N. Z. J. Crop Hortic.* 29:1-14.
- Huang, H. W. 2009. History of 100 years of domestication and improvement of kiwifruit and gene discovery from genetic introgressed population in the wild. *Chin Bull Bot* 44:127-142.
- James, D., and Phelan, J. 2016. Complete genome sequence of a strain of *Actinidia virus X* detected in *Ribes nigrum* cv. Baldwin showing unusual symptoms. *Arch. Virol.* 161:507-511.
- Liu, H., Song, S., Wu, W., Mi, W., Shen, C., Bai, B., and Wu, Y. 2019a. Distribution and molecular characterization of Citrus leaf blotch virus from *Actinidia* in Shaanxi Province, China. *Eur. J. Plant Pathol.* 154:855-862.
- Liu, H., Wu, W., Tan, J. Q., Li, Y., Mi, W. L., Jiang, L. J., and Wu, Y. F. 2019b. Development and evaluation of a one-step reverse transcription loop-mediated isothermal amplification for detection of Citrus leaf blotch virus. *J. Virol. Methods* 270:150-152.
- Loesch-Fries, L. S. 2021. Alfalfa mosaic virus (*Bromoviridae*). Pages 132-139 in: *Encyclopedia of Virology* (Fourth Edition), Vol. 3. D. Bamford and M. Zuckerman, eds. Academic Press, San Diego, CA, U.S.A.
- Martelli, G., Adams, M. J., Kreuze, J. F., and Dolja, V. V. 2007. Family *Flexiviridae*: A case study in virion and genome plasticity. *Annu. Rev. Phytopathol.* 45:73-100.
- Pearson, M. N., Cohen, D., Chavan, R., and Blouin, A. 2011. *Actinidia* is a natural host to a wide range of plant viruses. *Acta Hort.* 913:467-471.
- Peng, Q. D., Lv, R., Ning, J. C., Yang, T., Lin, H. H., Xi, D. H., and Zhuang, Q. G. 2019. First report of *Actinidia virus 1* infecting *Actinidia chinensis* in China. *Plant Dis.* 103:782.
- Peng, Q. D., Qiu, L., Yang, T., Ning, J. C., Xu, Q. Y., Dong, J. H., and Xi, D. H. 2020. A multiple reverse transcription PCR assay for simultaneous detection of four main viruses in kiwifruit. *Eur. J. Plant Pathol.* 156:1207-1212.
- Sawada, H., and Fujikawa, T. 2019. Genetic diversity of *Pseudomonas syringae* pv. *actinidiae*, pathogen of kiwifruit bacterial canker. *Plant Pathol.* 68:1235-1248.
- Thompson, J. R., Dasgupta, I., Fuchs, M., Iwanami, T., Karasev, A. V., Petrzik, K., Sanfaçon, H., Tzanetakis, I. E., van der Vlugt, R., Wetzel, T., Yoshikawa, N., and ICTV Report Consortium. 2017. ICTV Virus Taxonomy Profile: *Secoviridae*. *J. Gen. Virol.* 98:529-531.
- Veerakone, S., Lifting, L. W., Tang, J., and Ward, L. I. 2018. The complete nucleotide sequence and genome organization of a novel member of the family *Betaflexiviridae* from *Actinidia chinensis*. *Arch. Virol.* 163:1367-1370.
- Vives, M. C., Galipienso, L., Navarro, L., Moreno, P., and Guerri, J. 2001. The nucleotide sequence and genomic organization of citrus leaf blotch virus: Candidate type species for a new virus genus. *Virology* 287:225-233.
- Wang, D., Liu, X. X., Li, T. T., Li, Q., Liu, Y., Gong, G. S., and Yang, H. 2018. First report of cucumber mosaic virus infection in kiwifruit (*Actinidia chinensis*) in China. *Plant Dis.* 102:1180.
- Wang, R., Zhou, D., Luo, J., and Fang, J. B. 2017. Progress report on viruses of kiwifruit. *J. Fruit Sci.* 34:1043-1050 (in Chinese).
- Wang, Y. X., Hong, N., Wang, G. P., Yang, Z. K., Wang, L. P., and Li, L. 2016. First Report of the Tospovirus Tomato necrotic spot associated virus Infecting Kiwifruit (*Actinidia* sp.) in China. *Plant Dis.* 100:2539.
- Wang, Y. X., Zhai, L. F., Wen, S. H., Yang, Z. K., Wang, G. P., and Hong, N. 2020. Molecular characterization of a novel emaravirus infecting *Actinidia* spp. in China. *Virus Res.* 275:197736.
- Wang, Y. X., Zhuang, H. Q., Yang, Z. K., Wen, L. H., Wang, G. P., and Hong, N. 2018. Molecular characterization of an Apple stem grooving virus isolate from kiwifruit (*Actinidia chinensis*) in China. *Can. J. Plant Pathol.* 40:76-83.
- Wen, S., Wang, G., Yang, Z., Wang, Y., Rao, M., Lu, Q., and Hong, N. 2020. Next-generation sequencing combined with conventional sanger sequencing reveals high molecular diversity in *Actinidia virus 1* populations from kiwifruit grown in China. *Front. Microbiol.* 11:602039.

Guoding Zhang

Guoding Zhang is a master's degree candidate at the College of Plant Protection, Northwest A&F University, China. He graduated from the College of Plant Protection, Northwest A&F University with a bachelor's degree in 2021. His research interests are plant virus and phytoplasma diseases.

Bixin Bai

Bixin Bai is a doctoral candidate at the College of Plant Protection, Northwest A&F University, China. She graduated from the College of Innovation and Experiment, Northwest A&F University with a bachelor's degree in 2017. She works on plant virus and phytoplasma diseases.

Ming Xu

Ming Xu is a researcher responsible for kiwifruit breeding and cultivation technology research at the Shaanxi Province Rural Science and Technology Development Center. In 2014, he obtained a master's degree in biochemistry and molecular biology from Xinjiang Agricultural University.

Yuling Liu

Yuling Liu is an undergraduate student at the College of Plant Protection, Northwest A&F University, China. Her research focuses on virus detection and seedling detoxification of horticultural plants such as kiwifruit. She is also interested in aphids and aphid viruses, and has done research on the pathway of barley yellow dwarf disease in aphids.

Yunfeng Wu

Dr. Yunfeng Wu is a full-time professor at the College of Plant Protection, Northwest A&F University, China. He received his Ph.D. in 1994 from the Department of Plant Protection of Northwest Agricultural College in China. His research focuses on plant virus and phytoplasma diseases in field crops and fruit trees. He has published more than 150 scientific articles since 1994.

Lei Zhao

Dr. Lei Zhao is an associate professor of plant pathology in the College of Plant Protection, Northwest A&F University, China. He received his master's degree in 2013 and Ph.D. in 2016 from the College of Plant Protection of Northwest A&F University. His research focuses on plant virus and phytoplasma diseases in field crops and fruit trees. In addition, he is also interested in developments of new molecular methods for detection of viruses that infect vegetables and fruit trees. Since 2013, he has published more than 20 scientific articles in top international journals such as *Plant Disease* and *Molecular Plant-Microbe Interactions*.

- Wen, S. H., Zhu, C. X., Hong, N., Wang, G. P., Yang, Z. K., Wang, Y. X., and Wang, L. P. 2019. First report of *Actinidia virus 1* infecting kiwifruit in China. *Plant Dis.* 103:780.
- Woo, E. N. Y., Lebas, B., Veerakone, S., Tang, J., Ward, L., and Pearson, M. N. 2012. Molecular detection and characterisation of Cherry leaf roll virus in New Zealand. Page 48 in: 10th Australas. Plant Virol. Workshop, Hamner Springs, New Zealand.
- Wu, Y., Wang, Y., Sun, J., Liu, Y., Sujata, S., Wu, Y., and Lei, Z. 2022. Effects of *Actinidia* yellowing ringspot virus on the yield and quality of kiwifruit. *Plant Dis.* 106:800-804.
- Yang, C., Zhang, S., Han, T., Fu, J., Di Serio, F., and Cao, M. 2019. Identification and characterization of a novel *Emaravirus* associated with jujube (*Ziziphus jujuba* Mill.) yellow mottle disease. *Front. Microbiol.* 10:1417.
- Zhao, L., Cao, M. J., Huang, Q. R., Jing, M. P., Bao, W. W., Zhang, Y. L., Hou, C. T., Wu, Y. F., and Wang, Q. C. 2020. Occurrence and molecular characterization of *Actinidia virus C* (AcVC), a novel vitivirus infecting kiwifruit (*Actinidia* spp.) in China. *Plant Pathol.* 69:775-782.
- Zhao, L., Cao, M. J., Huang, Q. R., Wang, Y. C., Sun, J. X., Zhang, Y. L., Hou, C. T., and Wu, Y. F. 2021. Occurrence and distribution of *Actinidia* viruses in Shaanxi Province of China. *Plant Dis.* 105:929-939.
- Zhao, L., Hao, X. A., Liu, P., and Wu, Y. F. 2012. Complete sequence of an Apple stem grooving virus (ASGV) isolate from China. *Virus Genes* 45:596-599.
- Zhao, L., Yang, W., Zhang, Y. L., Wu, Z. M., Wang, Q. C., and Wu, Y. F. 2019. Occurrence and molecular variability of kiwifruit viruses in *Actinidia deliciosa* 'Xuxiang' in the Shaanxi Province of China. *Plant Dis.* 103:1309-1318.
- Zheng, Y. Z., Wang, G. P., Hong, N., Zhou, J. F., Yang, Z. K., and Hong, N. 2014. First report of *Actinidia virus A* and *Actinidia virus B* on kiwifruit in China. *Plant Dis.* 98:1590.
- Zheng, Y. Z., Navarro, B., Wang, G. P., Wang, Y. X., Yang, Z. K., Xu, W. X., Zhu, C. X., Wang, L. P., Serio, F. D., and Hong, N. 2017. *Actinidia* chlorotic ringspot-associated virus: A novel emaravirus infecting kiwifruit plants. *Mol. Plant Pathol.* 18:569-581.
- Zhu, C. X., Wang, G. P., Zheng, Y. Z., Yang, Z. K., Wang, L. P., Xu, W. X., and Hong, N. 2016. RT-PCR detection and sequence analysis of coat protein gene of citrus leaf blotch virus infecting kiwifruit trees. *Acta Phytopathol. Sin.* 46:11-16.
- Zou, M. F., Yan, M. F., Zhou, Y., Wang, Y. X., Xiong, G. H., and Jiang, J. X. 2020. First report of *Actinidia virus A* and *B* infecting kiwifruit in Jiangxi Province in China. *J. Plant Pathol.* 102:539.